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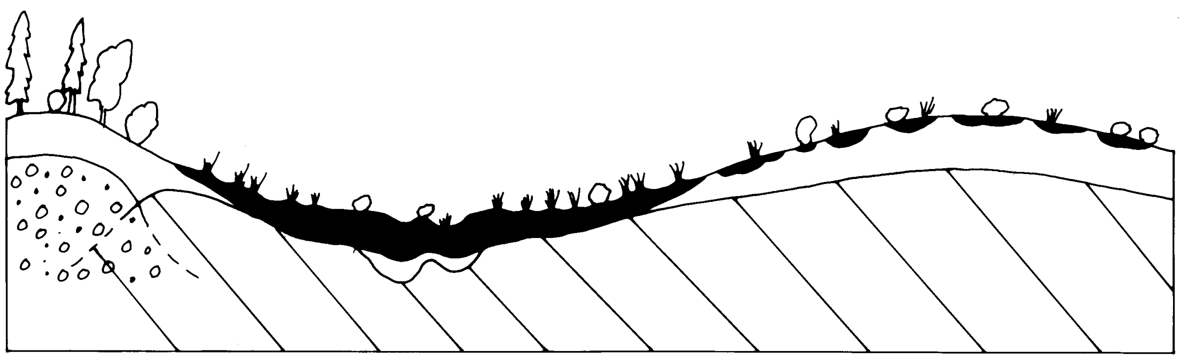
Technical Report NPS/AFA RNR/NRTR-96/28



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Abstract: The distribution of fruticose lichens in the upper Kobuk River valley is strongly influenced by soil conditions and disturbance; lichen cover is highest where disturbance is infrequent and poor soils reduce competition by vascular plants. Lichen cover is low on flooded soils as a result of burial by sediment and enhanced competition by deciduous vascular plants on rich floodplain soils. Lichen cover is also low on steep mountain slopes as a result of snow avalanche disturbance or dense vascular vegetation. Lichen cover is high on dry, stable, infertile soils unless there has been a recent burn. These soils occur mainly on bedrock ridges and on Pleistocene glacial deposits in the study area. Lichen cover increases for at least 100 years after fire on dry, unflooded soils; *Polytrichum* spp. moss and *Cladonia* spp. lichens dominate during the first half-century after fire, while *Cladina rangiferina* and *C. stellaris* lichens dominate thereafter. Wet soils generally have low to moderate lichen cover, probably as a result of competition by mosses and sedges. Exceptions include 1) palsas and peat plateaus, where droughty conditions due to drainage of water into thermokarst pits, and very acid soils allow lichens to dominate; and 2) sloping unforested areas in the lowland forest-tundra ecotone of the western part of the study area, where moss competition is apparently reduced due to lack of a tree overstory.

INTRODUCTION

Terrestrial fruticose lichens are locally quite abundant in the subarctic (Rowe, 1984). Several lichen species, notably those in the genus *Cladina* (Nyl.) Nyl., are important winter forage for caribou and reindeer (*Rangifer tarandus*; Holleman *et al*., 1979; Russell *et al*., 1993). Subarctic forests with dense lichen cover have been studied extensively in Canada, where they occur mostly on dry, infertile soils (Maikawa and Kershaw, 1976; Rencz and Auclair, 1978; Moore, 1980; Robinson *et al*., 1989). These lichen woodlands are fire-prone, and the valuable forage lichens require many years to recover after fire (Scotter, 1964; Black and Bliss, 1978; Johnson, 1981). Lichens in interior Alaska have received less attention. Christiansen (1988) studied tree growth and regeneration after forest fires in lichen woodlands near Walker Lake, adjacent to the present study area.

The present paper examines the distribution of terrestrial fruticose lichens in the Kobuk Preserve Unit, Gates of the Arctic National Park, as a function of environmental factors, primarily soil properties and natural disturbance. This information is presented in hopes that it will increase our understanding of lichen-rich winter range for caribou in the Kobuk Preserve Unit and elsewhere in interior Alaska.

STUDY AREA

The Kobuk Preserve Unit covers about 250,000 ha in northwestern Alaska south of the Brooks Range (Fig. 1). This region has a subarctic, continental climate. The nearest climatic station (Kobuk, Alaska, 40 km to the west) reports a mean July temperature of 14° C, mean January temperature of -23° C, mean annual temperature of -6°, and mean annual precipitation of 42 cm. Snow data for Bettles (100 km east of the study area) show maximum late winter (1 April) depth averaging 80 cm, with 18 cm of water stored in the snowpack (Soil Conservation Service, 1993).

Major physiographic features in the study area are highlands of the Brooks Range (along the northern border of the study area) and foothills of the Brooks Range; and broad valley bottoms with Pleistocene glacial moraines, and terraces and floodplains of the Kobuk River and its tributaries (Fig. 2). Moraines of three ages are present; the youngest is Late Pleistocene in age and the others are older but of unknown age (Fernald, 1964; Karlstrom *et al*., 1964; Hamilton, 1982). The youngest (Walker Lake-age) moraines are coarse-grained and lack a loess cover; older moraines have at least 0.5 m of silty

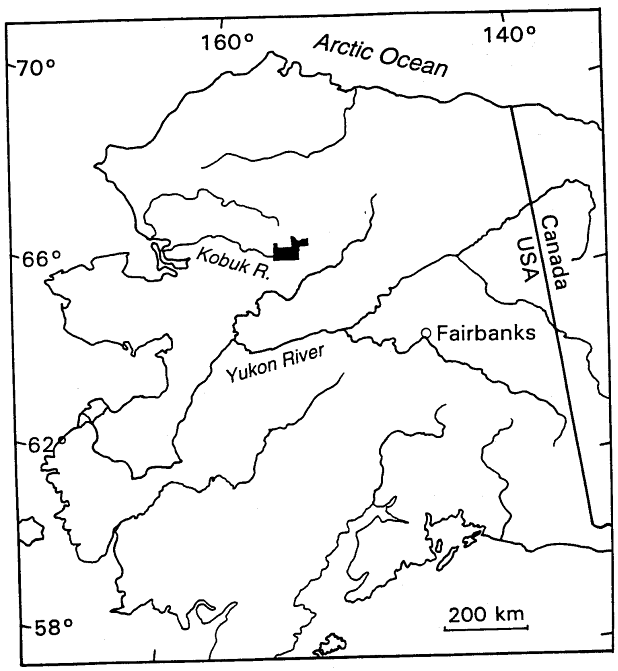

Fig. 1. Location of the Kobuk Preserve Unit, Gates of the Arctic National Park, Alaska.

Fig. 2. Landscape of the Kobuk Preserve Unit, Gates of the Arctic National Park. Major features, from the foreground to background, are: the Kobuk River, Kobuk River floodplain, moraines, foothills, and the Brooks Range.

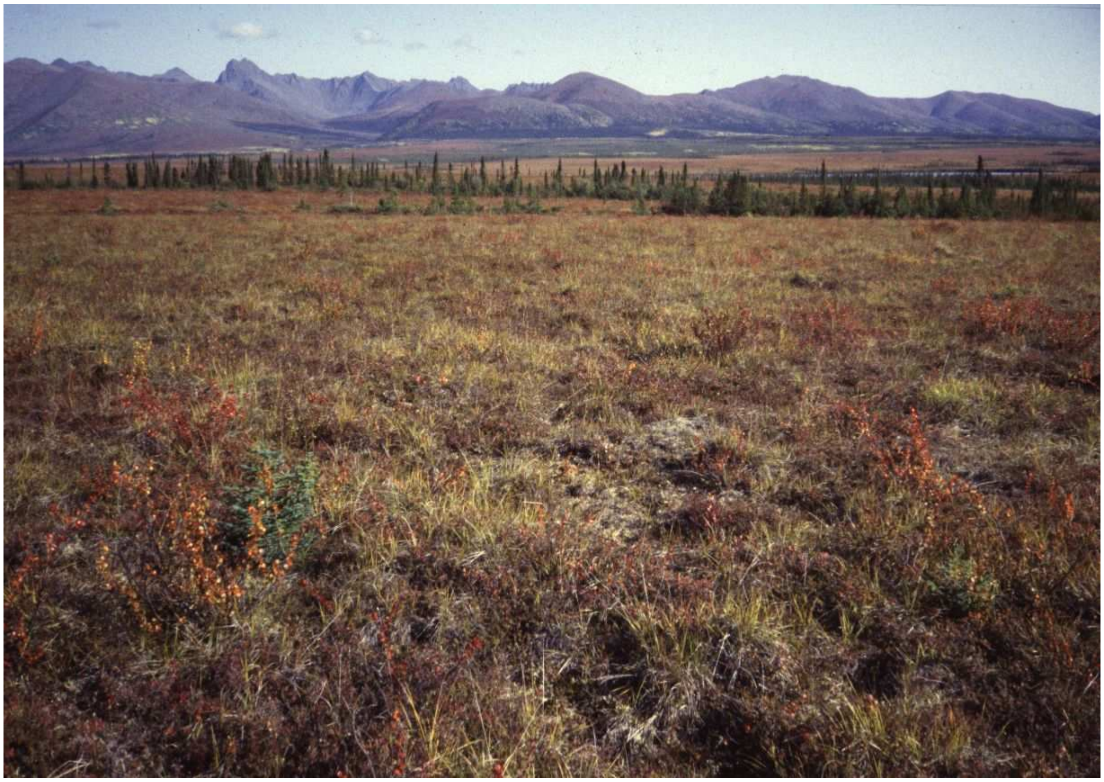

Fig. 3. Landscape of the forest-tundra ecotone in the western part of the study area. The foreground is mudboil tundra dominated by ericaceous shrubs, *Betula glandulosa, Carex bigelowii, Eriophorum vaginatum,* and *Cladina* spp. lichens (see Tables 3 and 4 for details). The trees are black spruce (*Picea mariana*). The soils here have a discontinuous organic surface layer up to 20 cm thick and permafrost at about 90 cm depth. The mineral soil is usually saturated. The Brooks Range is in the background.

loess over all except convex hilltops.

Bedrock in the study area, and the rocks composing the moraines, include a variety of volcanic, metamorphic, and sedimentary rocks, with small areas of limestone (Patton and Miller, 1966; Nelson and Grybeck, 1980).

Permafrost is widespread but discontinuous in the Kobuk Preserve Unit (Ferrians, 1965). It is generally absent only in dry, coarse-grained glacial and river deposits; some steep, south-facing slopes; and under lakes, rivers, and thaw ponds.

Vegetation in the study area is dominantly open black spruce (*Picea mariana*) forest. Black spruce may be accompanied by paper birch (*Betula papyrifera*) or aspen (*Populus tremuloides*), particularly on dry soils and in forests regenerating after fires. The understory of the black spruce forests includes various low shrubs, such as *Betula glandulosa*, *Vaccinium uliginosum, V. vitis-idaea*, and *Ledum palustre*, and ground cover of mosses and lichens. White spruce (*Picea glauca*) forest with alder (*Alnus crispa*) occurs locally on floodplains and on steep, generally south- or west-facing mountain slopes.

Tundra occurs in the mountains above 600 m elevation and in lowlands near the western border of the study area. The latter have a mosaic of forested and unforested vegetation referred to here as forest-tundra ecotone (Fig. 3). In the ecotonal area, nearly treeless patches occur on gentle slopes as well as on wet, level areas. In the taiga zone to the east, in contrast, slopes are nearly always forested. Trees within or on the fringes of the unforested patches in the ecotonal area show evidence of damage by windblown snow, which suggests that the treeless patches are indeed the result of a less favorable climate.

The study area falls within the wintering area of the Western Arctic caribou herd, although the main wintering grounds for this herd in recent decades have been further west (Pat Valkenburg, Alaska Department of Fish and Game, unpublished data).

METHODS

Field

Field data for this study were collected in the summers of 1992 and 1993 as a part of a landscape ecosystem mapping study (Swanson, 1995). Eighteen landscape ecosystem map units were defined and mapped at a scale of 1:63,360 by aerial photograph interpretation and field data collection. These map units encompass areas with a consistent pattern of landforms, soils, vegetation, and landscape-forming processes. Field data were collected along transect routes chosen from aerial photographs to cover representative and accessible areas of each map unit. Each map unit was divided subjectively into one to six major components with unique landscape setting, soils, and potential vegetation. Transect stations were located deliberately to ensure coverage of each major component. Because sample stations were located deliberately, they could be biased with respect to the frequency of any measured property (e.g. high lichen cover) in the study area. However, they still contain useful information about the relationship between lichens and other landscape properties.

Two levels of sampling intensity were used. Summary soil, site, and vegetation information was collected at 827 stations. Detailed vegetation descriptions were made at 255 of these stations, and detailed soils descriptions at 190 of these. The present article is based primarily on the 255 stations with intensive vegetation data.

Soil and site information collected at every transect station include soil classification to the family level (Soil Survey Staff, 1994); surface soil texture and two subsurface textures with depths to textural discontinuities (texture from Soil Survey Division Staff, 1993); elevation; slope steepness, aspect, and shape; major landform and position on the landform; geological material; organic surface layer thickness; depth to bedrock, frozen soil, water table, saturated soil, gleyed soil matrix, and gleyed soil mottles; and estimated flooding frequency (classes frequent >50 years in 100, occasional 5 to 50 years in 100, rare <5 years in 100, or none). All soil and site data were collected by a single observer.

Detailed vegetation descriptions were made for a roughly circular area within approximately 20 m of the soil pit. They include time since last fire (classes <10, 10-50, 50-100, >100 years); cover class of litter, soil, rock, water, total lichens, and total moss (classes <1, 1-5, 5-25, 25-50, 50-75, and 75-100%); canopy cover class of each species, or genus if species were not separable (classes as listed previously); and notes on use by wildlife (winter pellets, feeding craters, and trampled lichens in the case of caribou). The time since fire was estimated from tree cores and, for fires since 1956, unpublished US Department of Interior Bureau of Land Management fire records. Vascular plant names follow Hultén (1968), mosses Crum and Anderson (1981), and lichens Thomson (1984) except for *Cladina* (Nyl.)Nyl. All plant data were collected by a single observer.

Detailed soil descriptions include horizons symbols and depths, color, mottles, texture, structure, consistence, pH (by field color indicators), roots, and horizon boundaries (Soil Survey Division Staff, 1993).

Analytical

The relationship of total lichen cover to soil groups was examined using contingency tables and chi-square goodness of fit tests. Soil groups were obtained by combining soils judged to have similar environments for lichen growth. For the subset of soil groups with some records of high lichen cover, the relationship of total lichen cover to classes of time since fire was examined in a second contingency table. Cells in the contingency tables with counts higher or lower than expected were identified as those deviating more than *X* counts from the expected value, where:

$$X = nZ(p(1-p)/n)^{0.5}$$

n is the sample size, *Z* is the standard normal table value and *p* is the observed counts in the cell divided by n (Byers and Steinhorst, 1984). Two *Z* values were used, one corresponding to one standard deviation (Z=1; 1-tail P=0.16) and another corrected for the table-wide error rate using $Z=Z_{\alpha/k}$, where α is the probability value P=.05 and *k* is the number of cells in the contingency table. The first test identifies all cells with a reasonable probability of being higher or lower than expected, but up to 1/6 of all cells could be wrongly identified as unexpectedly high or low (type I error). The second, more stringent test is much less prone to type I errors, but subject to type II errors (failure to identify cells with counts higher or lower than expected).

The vegetation site types were composed as follows. Map units were separated subjectively into major components as described above. Each transect station was assigned to a component; unusual stations that did not fit well into any major component were considered to be "minor components". The vegetation site types were created by joining major map unit components with similar ecologic conditions for plant growth. A total of 30 vegetation site types was recognized, with one to 12 map unit components in each.

The vegetation site types correspond in general to the ecologic sites used in other resource inventories, such as the Seward Peninsula range survey (J.D. Swanson *et al*., 1985). I chose to call them "vegetation site types" rather than "ecologic sites" because the sample stations included in a given vegetation site type have similar conditions for plant growth, but not necessarily similar ecologic conditions in other respects.

Plant constancy was calculated as the percentage of transect stations in a vegetation site type where a plant was recorded. Mean plant cover where present was calculated using midpoints of the cover classes; only transect stations where the plant occurred were included.

RESULTS

Lichens and the Soil Groups

Lichen cover is clearly related to soil group (Tables 1 and 2). The total lichen cover reported here consists mainly of terrestrial fruticose lichens. Soils of group A support low lichen cover. This group contains organic soils without permafrost, which occur in thermokarst depressions and groundwater-discharge fens with the water table constantly near the surface. Soils of group B also support low lichen cover. This group contains all soils judged to be frequently or occasionally flooded (flooding frequency 5 or more years in 100) Soil groups C and D have mostly low to intermediate lichen cover. Both groups are soils with biochemically reduced mineral material (due to saturation), although the water table is not constantly at the surface as it is in the soils of group A. Group C contains soils with permafrost, a thick (>20 cm) organic surface layer, and rare or no flooding (flooding frequency less than 5 years in 100). Soil group D contains soils with less than 20 cm of organic surface material, mostly with permafrost, and rarely or never flooded. Soil group E has lichen cover generally higher than expected; it contains dry soils of all types with rare or no flooding.

A notable exception to the generally intermediate lichen cover on unflooded, wet soils (of group D) is the site type "Mudboil

Table 1. Count of lichen cover-class observations by soil group in the Kobuk Preserve Unit, Gates of the Arctic National Park[1]

Lichen cover, %					Soil Group[2]
0-5	5-25	25-50	50-75	75-100	
9^{+}	1^{-}	0^{-}	0^{-}	0^{-}	**A**: Organic, very wet, no permafrost
25^{++}	11	1^{--}	0^{-}	0^{-}	**B**: Flooded soils, wet and dry
9^{-}	24^{+}	19^{+}	11	2^{--}	**C**: Wet soils with permafrost and a thick organic surface
6^{-}	14	13^{+}	4^{-}	9	**D**: Wet mineral soils, mostly with permafrost
6^{--}	22^{-}	19	21^{+}	29^{+}	**E**: Dry soils
55	72	52	36	40	Total

$^{-,\,+}$ Count lower or higher than expected with cell P=0.16
$^{--}$, ++ Count lower or higher than expected with table-wide P=0.05
[1]Overall chi-square=126.5, df=16, P=0.0000
[2]For further explanation of soil groups, see Table 2

Table 2. Explanation of the soil groups

Taxa (count)

Group A: Organic soils, very wet, no permafrost
Histosols (10)

Group B: Flooded[1] soils, wet and dry

Aquents (6)	Fluvents (13)
Aquepts (10)	Umbrepts (1)
	Orthents (7)

Group C: Wet soils with permafrost and a thick organic surface
Histic Pergelic Cryaquepts (41)
Histosols (23)
Pergelic Ruptic-Histic Cryaquepts (3)

Group D: Wet mineral soils, mostly with permafrost

Aeric Cryaquepts (2)	Typic Cryaquepts (7)
Pergelic Cryaquepts (37)	

Group E: Dry soils

Aquic Cryochrepts (25)	Typic Cryochrepts (49)
Lithic Cryochrepts (2)	Typic Haplocryods (4)
Orthents (12)	Umbrepts (5)
Pergelic Cryochrepts (11)	

[1]Flooding frequent or occasional - more than 5 years in 100; all other soils have flooding rare or none - 5 or less years in 100

tundra", which occurs in nearly treeless areas on gently sloping moraines with deep silty soils and permafrost in the far western part of the study area (Figs. 3 and 4). This site type has high lichen cover and very little moss; in contrast, forested sites on similar landforms further east have a ground cover dominated by *Sphagnum* spp. mosses and feathermosses (mainly *Hylocomium splendens* and *Pleurozium schreberi*)(Tables 3 and 4). The median July-Aug thaw depth was 90 cm on the mudboil tundra (n=23) vs. 42 cm on the same landform in the taiga (n=16; n is larger here than in Table 3 because it includes the less detailed transect stations). Mudboil tundra occurs in patches many square kilometers in size; extensive burns have reduced lichen cover in some areas.

High lichen cover also occurs on some frozen organic soils (group C), those in site type "Palsas and peat plateaus" (Table 5, Fig. 5), although the small sample size (due to overall rarity of thick organic deposits in the study area) makes evidence anecdotal. These soils are droughty due to drainage into adjacent thermokarst depressions.

Lichens and Dry Soils

On the subset of dry soils (soil group E) that have been unburned for more than 100 years, lichen cover is related to vegetation site type (Table 6). A chi-square test would be unreliable on this table because of the numerous zero-value cells, but some trends are apparent. Low lichen cover occurs in snow avalanche tracks ("Avalanche tracks") and on shrub-rich forested mountain slopes ("Low mountain midslopes, unfrozen (forest)", and "Steep forested high mountain slopes").

High lichen cover occurs on the undisturbed dry sites with sparse vascular vegetation: "Dry terraces and uplands", "Dry crests and upper slopes of low mountains (forest and scrub)", and "Alpine tundra". These are dry, stable sites that occur below, near, and above treeline, respectively (Tables 4 and 6).

The most widespread dry-soil lichen site type, "Dry terraces and uplands", includes alluvial terraces, moraine ridges, and low bedrock ridges, usually with gravel near the surface. In the upper Kobuk Valley, gravelly alluvial terraces cover little area and occur in blocks of less than 1 km^2. Dry moraine and bedrock ridges (Fig. 6) generally occur in widely scattered, even smaller blocks surrounded by extensive black spruce forest with moss-dominated ground cover. The only rather large block of "Dry terraces and uplands" in the study area, i.e. at least several square kilometers, occurs on the youngest (Late Pleistocene) moraines just north of Nutuvukti Lake (Swanson, 1995). In contrast to the older moraines, these Late-Pleistocene moraines have no silty loess mantle, and thus dry, coarse-grained soils occur over much of the surface, rather than only on isolated ridgetops. A larger, gravelly Late Pleistocene moraine occurs south of Walker Lake (Christianson, 1988), just outside of the study area to the north. Most of these two large gravelly moraines currently have early successional-stage vegetation due to fires within the past 50 years.

Lichen Use by Caribou

Signs of winter use by caribou (pellets and feeding craters) are common on five of the vegetation site types (Table 4) out of the 30 site types that were recognized in this study. All except the "Pit and mound depressions, tundra" were mentioned above in connection with their high lichen cover; "Pit and mound depressions, tundra" is a minor site type similar to "Palsas and peat plateaus".

As discussed above, the most widespread lichen-rich site type, "Dry terraces and uplands", occurs as patches of lichen-rich habitat in an otherwise moss-dominated landscape. Some of these patches show no evidence of caribou use, while others have been heavily grazed and trampled to the point of exposing mineral soil.

Fire and Lichens

Lichen cover is also clearly affected by time since fire (Table 7). For soils capable

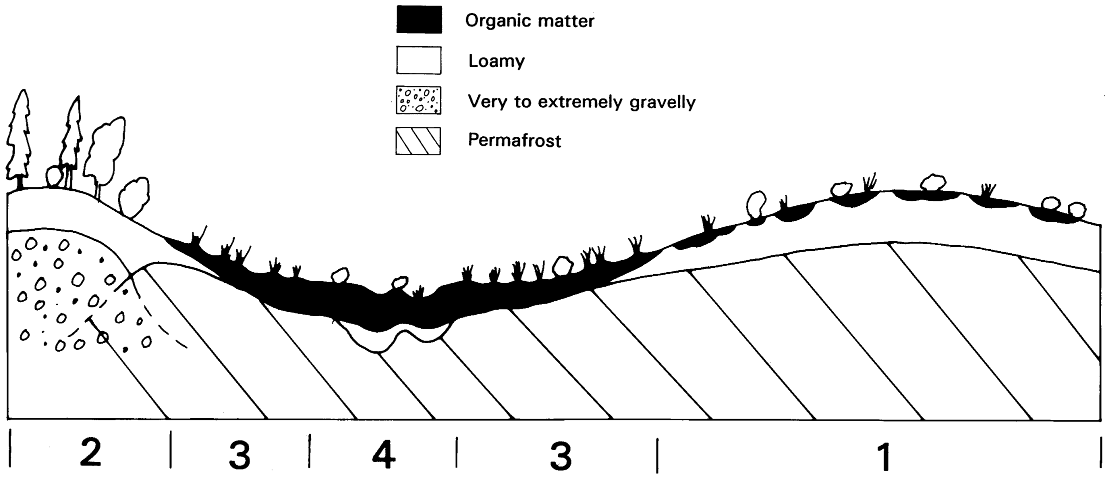

Fig. 4. Landscape diagram of the forest-tundra ecotone. Component 1 is vegetation site type "Mudboil tundra" (Tables 3 and 4); 2 is "Dry terraces and uplands", 3 is "Tussock tundra", and 4 is "Pit and mound depressions, tundra".

Fig. 5. Palsa and adjacent thermokarst depression. The palsa vegetation consists of black spruce, ericaceous shrubs, and *Cladina spp*. lichens (see Table 5 for details). The soil on the palsa is entirely organic matter, frozen at 44 cm depth on 29 July 1992 and lacked a water table on that date. The thermokarst depression has a mat of *Sphagnum* sp. moss, a graminoid layer dominated by *Carex aquatilis*, and very sparse ericaceous shrubs. The soil in the depressions consists entirely of organic matter, lacks permafrost, and had a water table near the surface on 29 July 1992.

Table 3. Constancy and cover of dominant plants on ecotonal mudboil tundra and analogous forested sites in the Kobuk Preserve Unit[1]

Plant Name	Constancy/cover, %	
	Tundra[2]	Taiga[3]
Trees		
Picea mariana	100/3	100/33
Shrubs		
Betula glandulosa	100/15	89/16
Empetrum nigrum	100/11	67/7
Ledum palustre	100/23	100/44
Vaccinium uliginosum	100/31	100/36
Vaccinium vitis-idaea	100/11	100/16
Graminoids		
Carex bigelowii	100/15	56/26
Carex spp.		44/32
Eriophorum vaginatum	100/11	33/14
Forbs		
Rubus chamaemorus	33/1	89/19
Mosses		
moss (total)	100/3	100/74
Hylocomium splendens		78/22
Pleurozium schreberi		78/15
Polytrichum spp.	100/1	78/13
Sphagnum spp.	67/3	100/46
Lichens		
lichen (total)	100/88	100/47
Cetraria cucullata	100/15	56/3
Cladina mitis	100/11	56/7
Cladina rangiferina	100/15	89/19
Cladina stellaris	100/31	89/21
N	3	9

[1]Dominant plants are those with constancy times cover greater than 10% for the tundra or taiga stations, or both; includes only sample stations with more than 100 years since last fire
[2]Site type "Mudboil tundra" (Table 4)
[3]Site type "Frozen moraines and terraces, forested"

Table 4. Summary properties of vegetation site types mentioned in text[1]

Alpine tundra - open low or dwarf shrubs over lichens (*Betula glandulosa*, *Ledum palustre*, *Loiseleura procumbens*, *Cladina* spp). On mountain crests and upper slopes with dry, coarse-grained soils

Avalanche tracks - tall shrubs over low shrubs over grass or moss (*Alnus crispa*, *Vaccinium uliginosum*, *Calamagrostis canadensis*). On steep mountain slopes with dry, coarse-grained soils

***Dry crests and upper slopes of low mountains (forest and scrub)** - open forest or woodland over shrubs over lichens (*Picea glauca*, *P. mariana*, *Betula papyrifera*, *Alnus crispa*, *Betula glandulosa*, *Ledum palustre*, *Vaccinium uliginosum*, *Cladina* spp.). On crests, shoulders, and upper slopes of bedrock uplands, near treeline with dry, coarse-grained soils

***Dry terraces and uplands** - open forest or woodland over low shrubs over lichens (*Picea mariana*, *Populus tremuloides*, *Ledum plaustre*, *Vaccinium uliginosum*, *Cladina* spp.). On crests and upper slopes of moraines and bedrock uplands, and on terraces, with dry, usually coarse-grained soils.

Frozen moraines and terraces, forested - open forest or woodland with low shrubs, graminoids, and moss (*Picea mariana*, *Ledum palustre*, *Vaccinium uliginosum*, *Carex* spp., *Sphagnum* spp.). On gentle crests and slopes of moraines and on terraces, with wet, silty soils with permafrost.

Low mountain midslopes, unfrozen (forest) - woodland or open forest over tall shrubs over low shrubs over moss (*Picea glauca*, *P. mariana*, *Betula papyrifera*, *Alnus crispa*, *Spiraea beauverdiana*, *Vaccinium uliginosum*, *Hylocomium splendens*). On slopes (usually south- or west-facing) of bedrock uplands with dry, coarse-grained soils.

***Mudboil tundra** - low scrub with graminoids and lichens (*Ledum palustre*, *Vaccinium uliginosum*, *Eriophorum vaginatum*, *Cladina* spp.). On gentle slopes and crests of glacial moraines in the far western part of the study area, with silty, wet soils with permafrost. Patterned ground of mudboils (nonsorted circles).

***Palsas and peat plateaus** (Zoltai and Tarnocai, 1975) - open forest or woodland with low shrubs, mosses, and lichens (*Picea mariana*, *Betula glandulosa*, *Ledum palustre*, *Vaccinium uliginosum*, *Sphagnum* spp., *Cladina* spp.). In level areas on moraines and terraces, with very acid peat soils with permafrost.

***Pit and mound depressions, tundra** - low scrub with graminoids, mosses and lichens (*Ledum palustre*, *Vaccinium* spp., *Eriophorum* spp., *Sphagnum* spp., *Cladina* spp.). On mounds between thermokarst pits in broad depression and flat areas on glacial moraines, with wet organic soils or organic over silty soils with permafrost.

Steep forested high mountain slopes - open forest with shrubs and moss (*Betula papyrifera*, *Picea mariana*, *P. glauca*, *Ledum palustre*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Hylocomium splendens).* On rubbly slopes (usually south- or west-facing) of high mountains protected by topography from avalanches, below treeline, with dry, coarse-grained soils

Tussock tundra - low scrub with graminoids and moss (*Ledum palustre*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Eriophorum vaginatum*, *Sphagnum* spp.). On gentle slopes and broad crests of glacial moraines in the far western part of the study area, on wet soils with thick organic matter over silty soil, with permafrost.

***Asterisk** indicates vegetation site type with numerous field notes of caribou pellets, feeding craters, and trampling of lichens.

[1]For more information on these site types, see Swanson (1995)

Table 5. Vegetation of an example transect stop on a palsa in the Kobuk Preserve Unit

Cover Class[1]	Name
15	litter
0	rock
+	soil
0	water
	Trees
15	*Picea mariana*
	Shrubs
15	*Betula glandulosa*
38	*Ledum palustre*
+	*Oxycoccus microcarpus*
15	*Vaccinium uliginosum*
15	*Vaccinium vitis-idaea*
	Graminoids
+	*Carex spp.*
3	*Eriophorum vaginatum*
	Forbs
38	*Rubus chamaemorus*
	Mosses
15	moss (total)
3	*Pleurozium schreberi*
15	*Sphagnum spp.*
	Lichens
88	lichen (total)
3	*Bryoria spp.*
+	*Cetraria cucullata*
+	*Cetraria islandica*
38	*Cladina rangiferina*
63	*Cladina stellaris*
+	arboreal crustose lichens

[1]+ indicates 0-1% cover, 3 is 0-5% cover, 15 is 5-25% cover, 38 is 25-50% cover, 63 is 50-75% cover, and 88 is 75-100% cover

Table 6. Lichen cover as a function of vegetation site type on unburned sites (>100 years since fire) with dry, unflooded soils (soil group E) in the Kobuk Preserve Unit

Lichen cover, %					Vegetation Site Type[1]
0-5	5-25	25-50	50-75	75-100	
0	0	0	2	3	Alpine tundra
0	2	0	0	0	Avalanche tracks
0	0	0	0	2	Dry crests and upper slopes of low mountains (forest and scrub)
0	0	1	6	14	Dry terraces and uplands
0	5	1	0	0	Low mountain midslopes, unfrozen (forest)
1	0	2	0	0	Steep forested high mountain slopes
1	1	2	0	1	Other minor site types
2	8	6	8	20	Total

[1]See Table 4 for an explanation of the vegetation site types

Fig. 6. Lichen-rich vegetation of the "Dry terraces and uplands" vegetation site type, more than 100 years after fire. The station is on the nearly level crest of a loess-covered, bedrock-cored hill. Trees are black spruce, and the ground cover is mostly *Cladina stellaris* lichens. The soil consists of 4 cm of organic matter over 60 cm of silt loam, over extremely gravelly sand, all unfrozen on 8 Aug 1992.

Table 7. Count of lichen cover class observations by time since fire on soil groups C, D, and E in the Kobuk Preserve Unit[1]

Lichen cover, %					Time Since
0-5	5-25	25-50	50-75	75-100	Fire, yr
5^{+}	7^{+}	0^{-}	0^{-}	0^{-}	0-10
5	28^{+}	21	10	4^{--}	10-50
0^{-}	3^{-}	6	6^{+}	4	50-100
11	22^{-}	24	20	32^{+}	>100
21	60	51	36	40	Total

[1]Chi-sq=49.3, df=12, P=0.0000; soil groups C, D, and E are those capable of supporting moderate to high lichen cover (see Tables 1 and 2)
$^{-,\,+}$ count lower or higher than expected with cell P=0.16
$^{--}$ count lower than expected with table-wide P=0.05

of supporting moderate to high lichen cover (soil groups C, D, and E), lichen cover is lower than expected for the first 50 years after fire, and higher than expected thereafter. Lichen species composition changes with time since fire (Table 8). The vegetation site type "Dry terraces and uplands", which has the largest sample size of any in the dry soil group, shows all lichens to have low average cover immediately after fire. *Polytrichum* spp. mosses and *Cladonia* spp. lichens dominate in the 10-50 year period. *Cladina rangiferina* and *Cladina stellaris* lichens dominate after 50 years, and increase from the 50-100 to >100 year classes. *Stereocaulon* spp. lichens peak in the 50-100 year range.

The dominant vascular plants on "Dry lichens and terraces" are black spruce and ericaceous shrubs (*Ledum palustre, Vaccinium uliginosum, V. vitis-idaea*). Aspen is conspicuous, but its average cover equals that of black spruce only for the first 50 years after fire, after which it decreases. Aspens trees occasionally show leaf dwarfing on these sites, probably due to nutrient deficiencies.

DISCUSSION

Factors Suppressing Lichens

The ability of lichens to tolerate drought and to subsist on minimal nutrients allows them to colonize very poor soils (Rowe, 1984). However, their very slow growth rates make them vulnerable to disturbance and to competition from other plants. Most records of low lichen cover in the study area can be attributed to disturbance (by flooding, fire, or snow avalanches) or competition from other plants, or both.

Flooding suppresses lichens by burial and mechanical damage, and by enhancing competition from other plants. In frequently flooded areas, lichens can be mechanically removed by flowing water and floating ice, and buried by sediment. Also, on floodplains growth of deciduous vascular plants such as willows (*Salix* spp.) and poplars (*Populus balsamifera*) is enhanced relative to unflooded sites (Viereck *et al*., 1983), and provides severe competition for slow-growing lichens. Deposition of fresh material by floods promotes growth of nutrient-demanding deciduous plants by enhancing soil fertility: soil pH is raised, often near to neutral, and organic matter is incorporated (by burial of surface litter) into the soil.

Fire is another well-known source of disturbance that reduces lichen cover. Destruction of lichens by fire and their slow recovery through successional sequences similar to the one reported here have been noted on the Seward Peninsula, western Alaska (J.D. Swanson *et al*., 1985) and in northern Canada (Scotter, 1964; Black and Bliss, 1978; Johnson, 1981).

Another source of disturbance that suppresses lichen growth is snow avalanching. Here both mechanical action and enhanced competition by deciduous vascular plants probably suppress lichens, as discussed above for flooding. Avalanche tracks support a rather dense vegetation of deciduous shrubs that out-compete lichens. Deposition of material by avalanches and mixing of soil by uprooting plants apparently enhances shrub growth by incorporating organic matter into the soil.

On steep mountain slopes with spruce forest and dense shrub understory, the mechanism of lichen suppression is probably mainly enhanced plant competition. Here the favorable microclimate on south- and west-facing slopes, and improved soil fertility by mixing of soil during creep on steep slopes, apparently are responsible for the dense vascular vegetation that suppresses lichens.

Very wet conditions are generally associated with sparse lichen cover, probably due to enhanced competition from mosses and sedges, and perhaps also to lichens' intolerance of submerged conditions. In thermokarst pits and groundwater discharge fens (soil group A), the water table is usually at the surface,

Table 8. Constancy and mean cover where present of non-vascular plants for various times since fire on the "Dry terraces and uplands" site type in the Kobuk Preserve Unit[1]

Name	Constancy/cover, %, by time since fire			
	<10yr	10-50yr	50-100yr	>100yr
Mosses				
moss (total)	100/12	100/35	100/20	100/25
liverwort	60/1	-	-	5/1
Aulocomnium palustre	-	15/2	-	-
Dicranum spp.	40/1	55/4	80/6	81/3
Drepanocladus uncinatus-	20/2	20/3	-	
Hylocomium splendens	20/3	5/3	60/6	43/9
Pleurozium schreberi	20/3	20/6	40/2	62/17
Polytrichum spp.	80/11	100/32	100/10	90/5
Ptilium crista-castrensis	-	-	-	5/1
Rhytidium rugosum	-	-	20/1	-
Sphagnum spp.	-	5/3	-	33/9
Tomenthypnum nitens	20/1	10/1	-	-
unknown moss	20/1	25/2	20/3	33/2
Lichens				
lichen (total)	100/10	100/41	100/73	100/78
Bryoria spp.	40/3	5/3	40/9	86/8
Cetraria (dark color)[2]	40/1	50/2	100/7	81/4
Cetraria cucullata	40/1	20/2	20/1	62/2
Cetraria islandica	-	-	-	19/2
Cetraria nivalis	20/1	25/2	20/1	24/7
Cladina mitis	-	35/3	60/11	38/9
Cladina rangiferina	20/3	25/5	100/13	100/24
Cladina stellaris	80/2	75/7	100/25	100/42
Cladonia spp.	80/2	95/18	80/21	100/1
Dactylina spp.	-	-	20/3	-
Nephroma arcticum	60/2	70/3	100/8	86/9
Peltigera spp.	20/3	65/8	40/3	62/2
Stereocaulon spp.	60/1	55/5	80/15	33/13
Usnea spp.	-	-	-	24/1
arboreal crustose lichens	40/1	35/1	80/3	57/2
soil crustose lichens	60/2	80/4	-	5/1
unknown lichen	40/15	-	-	5/1
N	5	20	5	21

[1]Constancy is the percent of transect stops where the plant was recorded; cover where present was calculated only from transect stops where the plant was recorded
[2]May include *C. islandica, C. ericetorium, C. laevigata, C. delisei*, or *C. Kamczatica*

Sphagnum mosses form a continuous mat and lichens are rare. *Sphagnum* spp. mosses, and feathermosses (mainly *Hylocomium splendens* and *Pleurozium schreberi*) thrive on the wet soils of groups C and D, apparently restricting lichen cover by competition. On some soils of groups C and D (where moisture and nutrients are sufficient), cottonsedge (*Eriophorum* spp., mostly *E. vaginatum*), dominates the microtopographic highs and provides further competition for lichens. As discussed below, well-drained microtopographic highs in wetlands may have high lichen cover.

Properties of Lichen-Rich Sites

The dry, stable, infertile sites of types "Dry terraces and uplands" "Dry crests and upper slopes of low mountains (forest and scrub)", and "Alpine tundra" provide lichens with protection from disturbance (except for fire) and from excessive plant competition. Dryness probably limits competition by mosses. Vascular plant biomass is low (Rencz and Auclair, 1978), probably due to low soil fertility (Moore, 1980) and lack of moisture. In alpine areas, high winds also limit vascular plant density. Low fertility apparently inhibits growth of drought-adapted vascular plants such as grasses, resulting in dominance among the vascular plants of nutrient-conserving ericaceous shrubs and (below treeline) black spruce; these are the same vascular plants that dominate very acid wetlands. High lichen biomasses were also reported on a variety of stable, dry sites with coarse-grained soils on the Seward Peninsula by J.D. Swanson *et al*. (1985) and in northern Canada (Johnson, 1981; Rowe, 1984).

The chemical reasons for poor soil fertility in dry, stable subarctic soils are not entirely clear. Low cation-exchange capacity due to low clay and organic-matter content of mineral soils is clearly a factor (Moore, 1980). Acidification and leaching of soils on stable sites are also probably contributing factors (Moore, 1980). In the study area, surface organic horizon, where most roots are located, are very acid (pH 4 to 5). However, strong leaching does not take place in the Kobuk Valley, as shown by pH values in the 5-6 range just below the mineral soil surface, and by the overall rarity of Spodosols. The enhanced productivity on soils where organic matter is buried (by flooding, downslope movement of soil, or animal burrowing) suggests that poor incorporation of organic matter into the mineral soil may be an important factor in low soil fertility in the subarctic.

The high lichen cover on mudboil tundra is an interesting exception to the generally low to intermediate lichen cover on wet, frozen soils. The immediate reason for denser lichens in the mudboil tundra than analogous taiga sites is apparently reduced competition by mosses on the tundra. The following explanation is proposed for low moss cover in these tundra areas. First, note that even on forested sites with permafrost, where mosses generally thrive (such as the taiga stations in Table 3), *Sphagnum* spp. mosses do not form a continuous cover wherever drainage is facilitated by some surface slope. Moisture is apparently insufficient to allow *Sphagnum* to dominate entirely on uplands, and hence feathermosses are also needed to maintain the surface organic mat that in turn maintains a high permafrost table and keeps the soil wet enough for *Sphagnum*. Feathermosses, however, grow best with nutrients supplied by tree canopy drip (Moore, 1980; Johnson, 1981), and thus do not grow densely on the tundra. Therefore, the lack on the tundra of feathermosses to "reinforce" the high permafrost table leads to deep summer thaw and better drainage, restricting *Sphagnum* to the very wet areas (such as the tussock tundra in Fig. 4). The extensive gentle uplands are thus open to domination by lichens. High lichen biomasses were also reported for ecologic sites on the tundra of the Seward Peninsula with frozen, rather wet soils but topographically facilitated drainage (e.g. "Lichen-sedge meadow (upland)").

The dense lichen cover on some

palsas and peat plateaus is apparently due to drainage of water into adjacent thermokarst depressions and consequent reduced competition from less drought-tolerant *Sphagnum* mosses. The extremely acid soils of these ombrotrophic peatlands also restrict competition from most vascular plants. High lichen biomasses were reported for similar sites on the Seward Peninsula: ecologic site "Spruce-lichen (palsa)" (J.D. Swanson *et al*., 1985).

Implications for Caribou Range

The dense lichen stands on dry, unflooded, sparsely forested soils in the study area provide winter range for caribou. However, these "lichen woodlands" are not nearly as extensive in Alaska as in northern Canada (Maikawa and Kershaw, 1976; Rencz and Auclair, 1978; Johnson, 1981; Rowe, 1984). The reason is that much of northern and central Alaska was not glaciated in the Late Pleistocene (Péwé, 1975), while nearly all of Canada was. The references cited above show that coarse-grained, Late Pleistocene glacial deposits with dense lichens are widespread on the Canadian shield. In contrast, fine-grained, loessal soils, which develop outside of the glaciated areas during glaciation, are more widespread in central and northern Alaska than the well-drained, sandy and gravelly glacial deposits that support the best taiga lichen stands. Coarse-grained glacial deposits in northern and central Alaska are restricted mainly to valley bottoms in the vicinity of the Alaska and Brooks Ranges. In unglaciated parts of the Alaskan taiga, the dry, unflooded soils favorable to lichen growth are generally restricted to narrow bedrock ridgetops.

In short, the restricted occurrence of dry, coarse-grained soils in interior Alaska prevents extensive lichen woodlands from developing and forces caribou to winter on other types of range, such as those described below. Also, the occurrence of lichen woodland in small patches that caribou may or may not find apparently leads to uneven use: patches within several kilometers of one another may be untouched or very heavily grazed.

Areas of lichen-rich tundra in the tundra-forest ecotonal region may also provide important wintering range for caribou in western Alaska. As discussed in the previous section, Alaska's dominantly fine-grained soils should not restrict lichen growth in the ecotone as much as in the taiga. The wetter, herb-dominated tundra associated with the lichen-rich tundra (Fig. 4) probably supplies caribou with the winter-green graminoid forage they need to round out the carbohydrate-rich and highly digestable but nutrient-poor lichens (Klein, 1982). The extent and character of the tundra-forest ecotone in western Alaska is not as well studied as the analogous region in northern Canada (Larsen, 1989; Payette and Lavoie, 1994).

Though palsas and peat plateaus are not extensive in the study area, my observations suggest that they (especially peat plateaus) cover large areas of lowlands in interior Alaska and may constitute important wintering habitat for caribou. The wet thermokarst depressions associated with palsas and peat plateaus (Fig. 5) probably supply caribou with the winter-green herbaceous vegetation to supplement lichens as discussed above.

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